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COOPERIA TOTADENTATA, A REMARKABLE RHINOCEROS FROM THE EOCENE OF MONGOLIA¹

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A large number of interesting undescribed rhinocerotoids, collected by the Central Asiatic Expeditions, were assigned to me for study and description by the late Professor Henry Fairfield Osborn and Dr. Walter Granger of the Department of Vertebrate Palaeontology of The American Museum of Natural History. The important but rather isolated and perplexing specimen which forms the subject of this paper was identified as a titanotherine in the field and as an amynodont, following preparation. Study showed, however, that it is an altogether new type of rhinoceros without close resemblance to any previously known form.

I am indebted to Dr. Granger for information dealing with the stratigraphy of this and other finds and to Mr. Jack N. Peterman for the accompanying original drawings.

RHINOCEROTIDAE

COOPERIA, NEW GENUS²

TYPE SPECIES.—*Cooperia totadentata*, described below.

DIAGNOSIS.—Size of large species of *Trigonias*, e.g., *T. gregoryi*; nasals smooth, slightly convex dorsally from front to rear and, more markedly, from side to side, with anterior tips not retracted but forming a stubby triangle; posterior end of nasal incision above canine; premaxillaries somewhat deflected, anteriorly; I^3 , C^1 , P^4 , M ; $C^1 > I^2 > I^3$; I^3 caniniform; canine stubby, large, not hypertrophied; none of premolars molariform— P^2 most progressive, followed by P^3 , then P^4 ; P^1 extremely primitive, composed principally of parametacone (or amphicone), with small basal protoloph and still lower antero-internal cingulum; P^{2-4} have paracone and metacone, and P^{3-4} have parastyle, as well, forming strong external ribs on the ectoloph, with the paracone rib most prominent throughout; protoloph and metalophs of P^{2-4} converge into V's, which are modified by partial separation of hypocone in P^2 , and by incomplete fusion of metaconule and protocone in P^4 ; P_4 inferred to have been considerably shorter than either P_2 or P_3 .

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No. 136 of this series is Novitates No. 939, the serial number of which was inadvertently omitted. Ed.

² This name recognizes the valuable work of Mr. C. Forster Cooper on the fossil rhinoceroses. It is also designed to suggest relationship to the baluchitheres in a manner without unfortunate connotations if this inference be hereafter disproved.

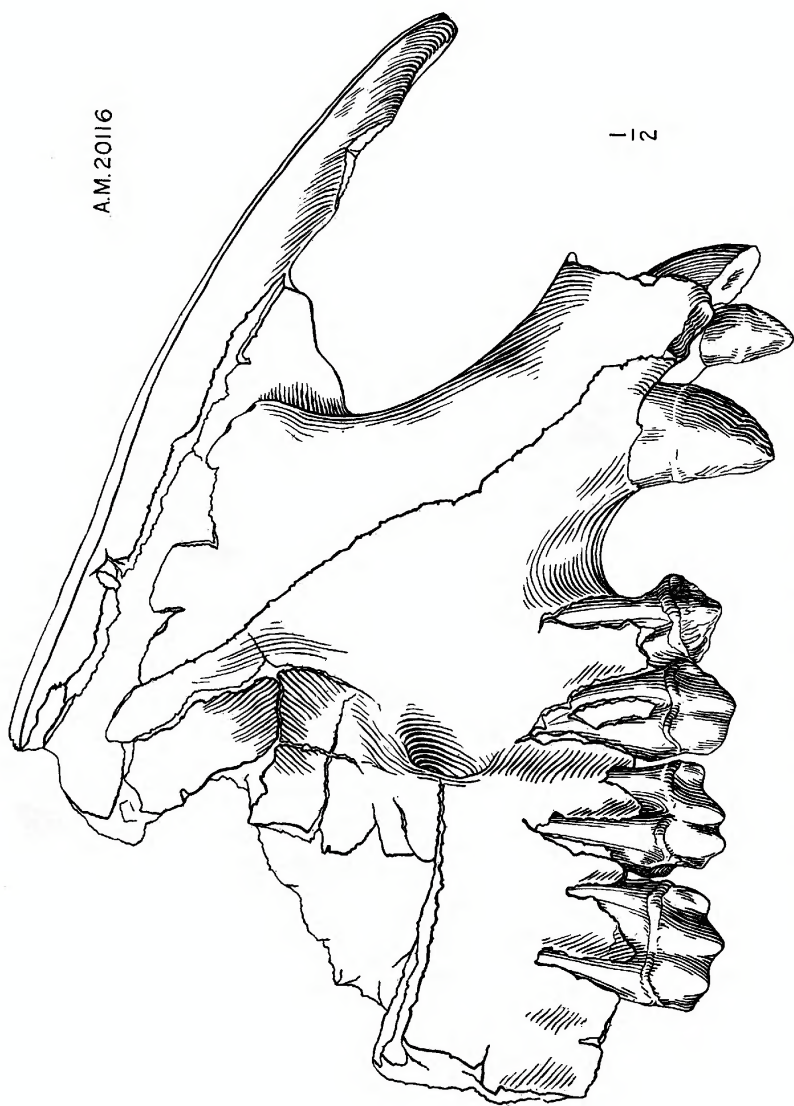


Fig. 1. *Cooperia totadentata*, right side, A.M.N.H. No. 20116, $\times \frac{1}{2}$.

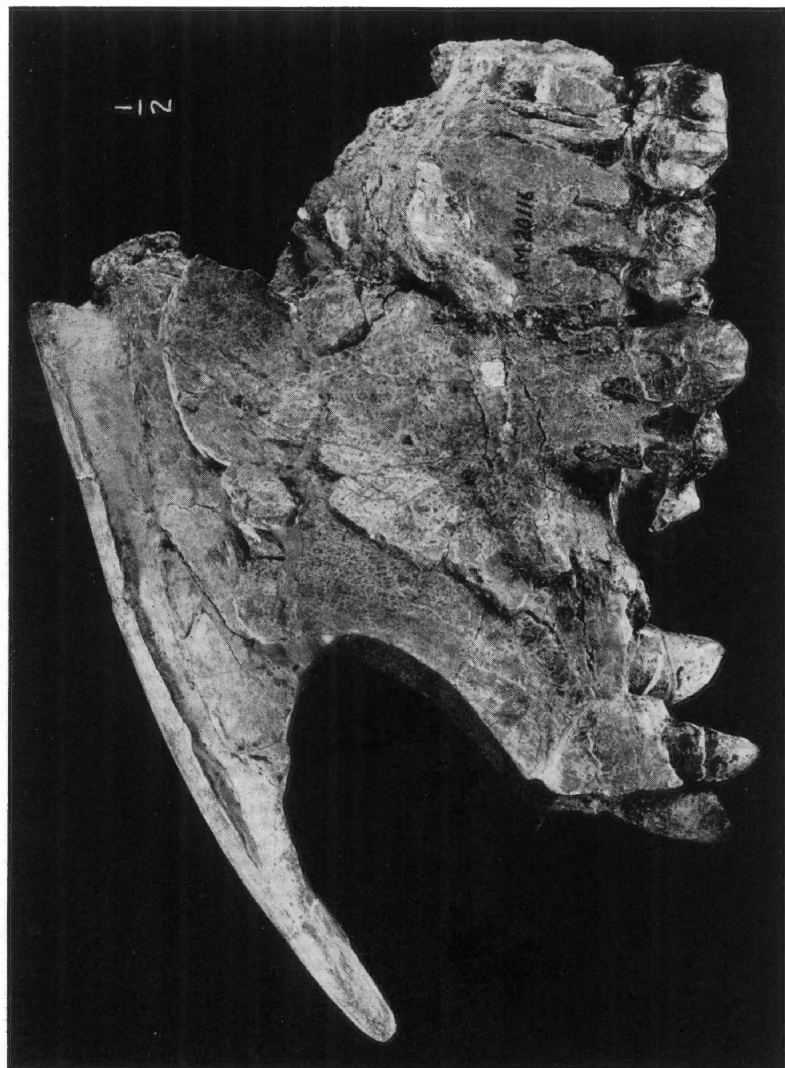


Fig. 2. *Cooperia totadentata*, left side, A.M.N.H. No. 20116, $\times \frac{1}{2}$.

***Cooperia totadentata*, new species¹**

TYPE.—A.M.N.H. No. 20116, front of skull with all premolars and some front teeth, collected by George Olsen, June 5, 1923, Field No. 173.

HORIZON.—Irdin Manha Formation, Upper Eocene.

LOCALITY.—Telegraph Line Camp, 2 miles north of line, Irdin Manha Bench, 23 miles southeast of Iren Dabasu, Inner Mongolia.

DIAGNOSIS.—Only known species of genus; measurements given below.

OSTEOLOGY

The severe lateral crushing to which the skull had been subjected obscures some characters. The tips of the nasals form a blunt isosceles triangle, as in *Hyrachyus* and *Amynodon*, but are not retracted, ending about above the first incisor as in hyrachyids and many true rhinoceroses, but unlike hyracodonts and amynodonts. The nasals apparently lack lateral notches and lack any indication of horn rugosities. The curved dorsal profile is not exactly like any other rhinoceros, and the angulation between the dorsal profile and the dental plane of occlusion is unreliable, as the premaxillaries and maxillaries have been telescoped over the nasals, probably more so anteriorly than posteriorly, thus increasing the angle between tangents to the two surfaces by an undetermined amount. The curve of the profile does not seem distorted and is vaguely amynodont, but the length of the arc suggests the baluchitheres only (Figs. 1-2). Its sweep in *Cooperia* is readily derivable from the primitive hyrachyid condition, and could readily give rise to the baluchithere condition as restored by Granger and Gregory (1936) in less exaggerated and, I believe, more accurate form than in previous restorations. The posterior end of the nasal incision is above the canine. This incision is more prominent than in *Hyrachyus*, shows some resemblance to *Amynodon* and is less prominent than in the baluchitheres. It is very different from *Trigonias*, *Subhyracodon* or similar primitive but already unmistakable true rhinoceroses in which the characteristic shape of the facial region is due to the sharp, oblique angle between the descending rim of the premaxillary and the nearly horizontal dorsal edge of the anterior end of the same bone in front of the premolars, to which the ventral border is parallel. This condition is characteristically rhinocerotid and is not found in the other families, although it is also modified in some later specialized rhinocerotids. The tips of the premaxillaries are missing so that their original relation to each other is uncertain, but they were probably fairly long and in contact. Enough is preserved, particularly

¹ The specific name indicates the presence of the primitive placental tooth formula without reduction so far as the evidence goes.

on the left side, to suggest a down-turned anterior end of baluchithere type, but much less pronounced in degree. This is shown not only by the angulation of the ventral border of the premaxillary with the occlusal plane of the premolars but also by the fact that the gum-line on the root of left I^2 is deflected about four millimeters ventrally below the gum-line of I^3 with reference to the premolar occlusal plane (Figs. 1-2). This deflection of the premaxillaries does not seem to be due to crushing but it is impossible to be positive about so badly distorted a specimen. The premaxillary-maxillary sutures pass a short distance in front of the canines. The lateral crushing of the skull tends to obscure the original skull proportions, giving a probably fictitious (or, conceivably, merely exaggerated) appearance of the presence of preorbital pits comparable to those of *Amynodon advenus*, and telescoping the dorsal rims of the premaxillaries and maxillaries over the ventral borders of the nasals (Figs. 1-2). The infraorbital canal widens, posteriorly, and opens, anteriorly, above the front of P^3 , on the side of the face, as in true rhinoceroses, not in the presumably artificial "preorbital fossa" as it should if it were an amynodont. The diastema is short as in primitive forms which have not lost nor atrophied any of the teeth, e.g., *Hyrachyus*, but this character is not especially diagnostic: for example, this condition is not very different from that in *Hyracodon*. The incisive foramen appears to have been long and narrow, but this, also, cannot be regarded as certain; and the palate is so badly crushed together that no data can be obtained, except the unexciting fact that a hard palate was present.

DENTITION

The calcareous deposit on the teeth must not be confused with cement, as it includes sand grains similar to those in the remains of the quartzose sandstone matrix which still adheres to the specimen. The teeth are unworn or barely worn. The tips of the premaxillaries are broken off, leaving only the base of the alveolus of I^1 , right. I^1 could hardly have been a small tooth, as the root was evidently comparable to that of I^2 in length; it is not clear whether the tooth was larger or smaller than I^2 (Fig. 3). It could hardly, however, have been an enlarged tooth of rhinocerotid type—at least, if so, the root was of the type found on a sharply-pointed incisor. The base of the root of I^2 , right, and the entire root of I^2 , left, are preserved. The circumference is considerably greater than for I^3 at comparable levels, considerably smaller than for the canine. The apex of the root is strongly curved to the rear, recalling the condition in the incisors of *Amynodon advenus*. However, no special

significance attaches to this fact, as the condition is even more similar in the enlarged I^3 of the living tapirs (e.g., *Tapirus indicus*, A.M.N.H. No. 80077, and *T. terrestris*, A.M.N.H. No. 36661). This appears to be a mechanical necessity whenever the root is longer than the vertical depth of the premaxilla. I^3 , right, had dropped out of the alveolus after death and before fossilization; I^3 , left, is unworn, small, simple, stubby, essentially caniniform, with anterior and posterior flanges and with a few vertical ribs barely indicated on the antero-external face. The left canine, like I^3 , right, had dropped out after death; the right canine is

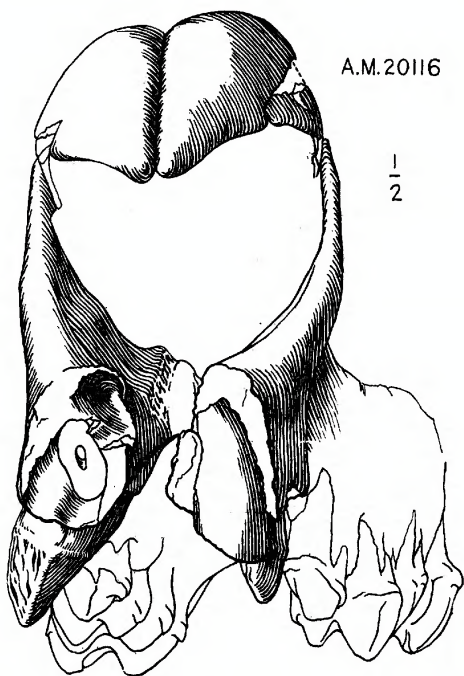


Fig. 3. *Cooperia totadentata*, anterior end of skull, A.M.N.H. No. 20116, $\times \frac{1}{2}$.

short, stubby, pointed, with flanges front and rear and a short median flange at the tip, with the antero-external surface between the flanges showing a vertical, rugose ribbing even coarser than that on P^1 . On any basis of comparison, the canine is markedly larger than either I^3 or I^2 ; the relation to I^1 is not so clearly demonstrable, but the canine was probably larger (Figs. 1, 3 and 4).

As the first right and left premolars of this specimen are less worn

than the other premolars, they are treated as members of the permanent series. None of the premolars are yet molariform (Figs. 4 and 5B). P^2 is the most progressive, followed by P^3 , then P^4 and then, at a long interval, by the extremely primitive P^1 . The premolars show no special amynodont features; on the contrary, they are similar to primitive true rhinoceros premolars in general, and suggest those of *Trigonias* and the *baluchitheres* in almost every character (Fig. 5). P^1 has a single main cusp, the parametacone or amphicone, with flanges front and rear. The external slope of the ectoloph carries coarse, vertical ribs. The external cingulum is narrow but continuous. The protoloph, apparently of cin-

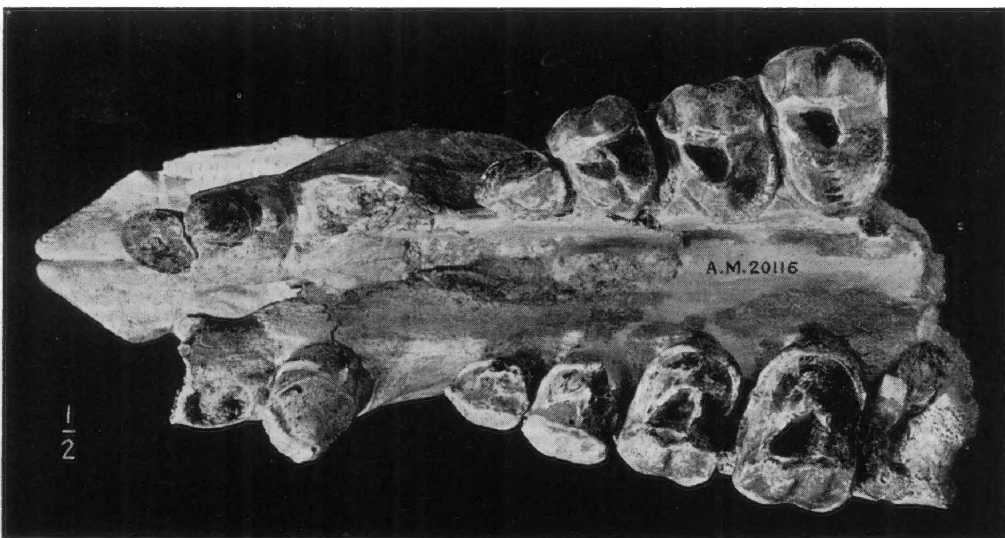


Fig. 4. *Cooperia totadentata*, palate, A.M.N.H. No. 20116, $\times 1/2$.

gular origin, forms a rib down the internal slope of the parametacone, swings around the internal edge of the cusp and becomes nearly (P^1 , left) or entirely (P^1 , right) confluent with the posterior cingulum. A lower antero-internal cingulum goes from the clearly defined parastyle (usually less defined) about to the junction of the protoloph and postero-internal cingulum. Minor ribs on the internal slope of the parametacone represent the sites of the potential crista and metaconule, respectively, the "metaconule" being the more prominent of the two. There is also an internal rib on the main cusp, just behind its junction with the parastyle. P^2-4 show double, strong ribs, the paracones and

metacones, on the external slopes of the ectolophs, the anterior (paracone) ribs being the more prominent. The external cingula are prominent at the base of these cusps but interrupted between them. The premolar parastyles, of nearly normal rhinocerotid type (i.e., not hyrachyid), become progressively more prominent from front to rear, being unusually everted and clearly defined by parastylar grooves on P^{3-4} , as compared with true rhinocerotids in general. The attachment of the protoloph to the ectoloph becomes progressively higher on the crown and more intimate from P^1 to P^4 . However, it is not really low on P^2 , where it is of the primitive, true rhinoceros type and definitely not hyrachyid. The attachment of the metaconule to the metacone is high and very similar on P^{2-4} , giving various modifications of the V-pattern. The hypocone of P^2 is partly budded off from the protocone and is about equally attached to the protoloph and the metaconule. A minute crochet is present. The median valley is an enclosed medifossette, with the anterior "wind-gap" between the protoloph and ectoloph slightly lower than the posterior one over the middle of the metaconule. The crista of P^2 , left, is a thin ridge, double proximally; P^2 , right, has hardly any crista but a similar condition is barely indicated. The cingulum continues from the anterior side, internally and then posteriorly, but nearly merges into the internal slope of the protocone at its internal end. The internal end of the protoloph (protocone) of P^3 is recurved and curves slightly posterior to the internal end of the metaconule, but shows no trace of a differentiating hypocone. A posterior groove descends buccal as the boundary between the protocone and metaconule. The medifossette seems deeper than on either P^2 or P^4 , but is actually a little shallower than on P^4 . The transverse crests of P^3 approximate a V with a blunted apex, and the transverse lophs form a more nearly continuous crest than in the other premolars. There is a small crista on P^3 , left, barely indicated on P^3 , right. The internal cingulum is briefly but definitely interrupted at the protocone. P^{3-4} , right, have small ribs which might be called crochets, except that they occur exactly at the junction of the metaconule and ectoloph. These ridges are absent on the left side. P^4 is generally similar to P^3 but is larger, and the metaconule is less firmly joined to the protocone, as the median valley has a partial outlet to the rear over a high saddle. The metaconule is more curved than in P^3 . Both P^4 s show the faintest trace of an internal groove, basally, incipiently delimiting the hypocone from the protocone. As usual, the tooth is somewhat rounded off, postero-internally, as compared with P^3 . The cingulum should probably be described as tenu-

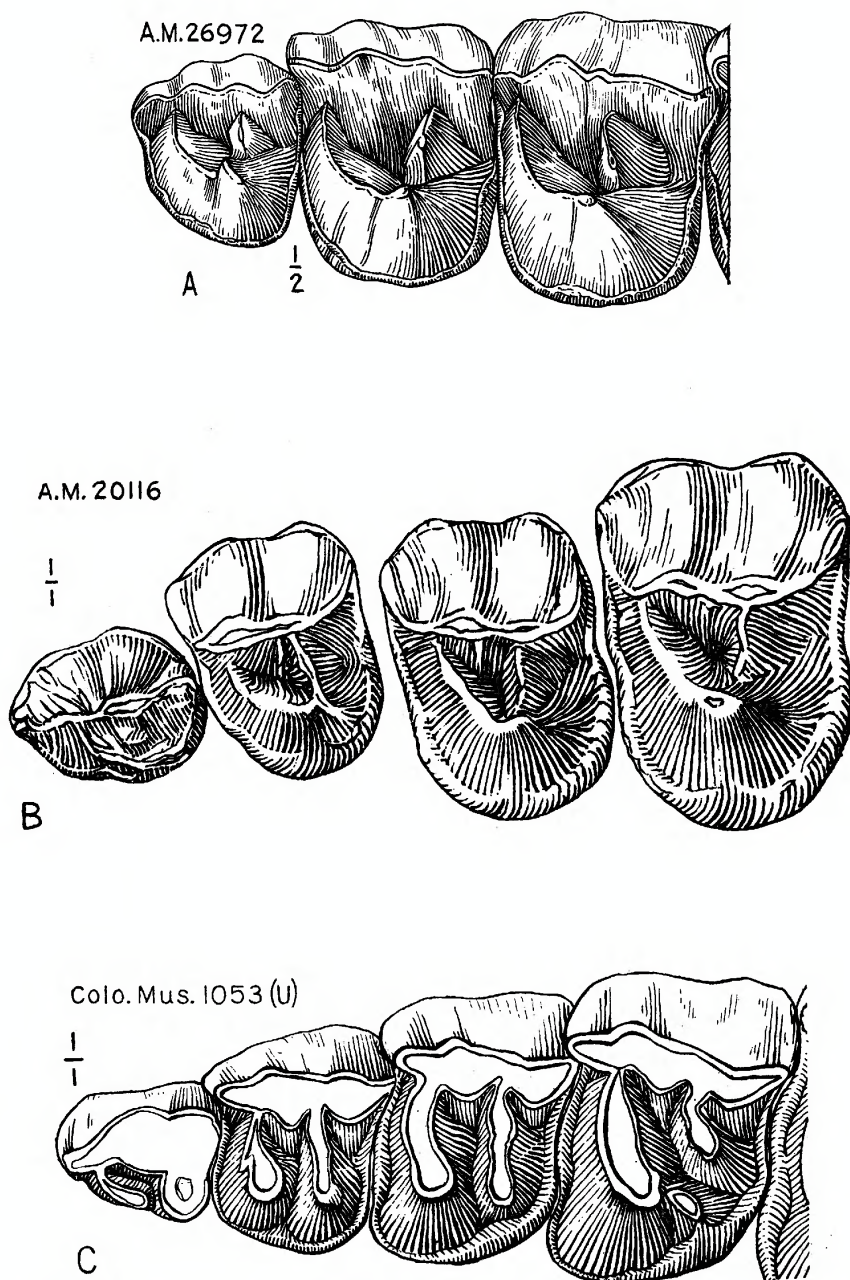


Fig. 5. A, *Indricotherium asiaticum* Borissiak, right P^{2-4} , reversed, from cast, A.M.N.H. No. 26972, after Granger and Gregory, $\times \frac{1}{2}$. B, *Cooperia totadentata*, P^{1-4} , left, A.M.N.H. No. 20116, $\times 1$. C, *Trigonias cooki* Wood, P^{1-4} , left, Colorado Mus. No. 1053 (U), $\times 1$.

ously continuous internally rather than as barely interrupted by the protocone. All three rear premolars suggest *Trigonias*, but P^4 shows the closest resemblance (Fig. 5B and C).

INFERRED CHARACTERS OF LOWER TEETH

In view of the importance and anomalous character of this specimen it is desirable to formulate such inferences regarding the lower dentition as can safely be drawn from the amount and location of wear on the upper teeth, from the boundary angles between the wear facets for the respective lower premolars, and from the requirements for normal occlusion with the upper teeth.¹ As I^3 and C^1 are unworn, the lower canine can hardly have been hypertrophied on the amynodont pattern and may well have been somewhat smaller than the upper canine. P^1 is noticeably worn only behind the tip of the parametacone indicating that P_1 was probably small or absent. Right P^1 is faintly worn anteriorly and left P^1 quite unworn, which appears to indicate either the absence of P_1 , left, or, rather more probably, that a small P_1 was present on both sides. Since the whole ectoloph of P^2 is worn, whereas the whole internal portion of the tooth is unworn except at the external end of the metaconule, it may be inferred, with considerable confidence, that P_2 was a primitive tooth consisting primarily of an antero-posterior blade composed of the protoconid and hypoconid. It must have been about 28.5 mm. long. The ectoloph of P^3 is well worn and the protoloph slightly, on each side, also the right metaconule, that of left P^3 being unworn. Evidently P_3 had asymmetrical trigonid and talonid crescents of rhinocerotoid type, the trigonid being much higher. The hypoconid was still the main talonid cusp, with the anterior limb lower than the postero-external corner, and the posterior limb of the talonid crescent dropped rapidly to or toward the cingular level, much as in P_4 of *Hyrachyus*. P_3 was approximately 30 mm. long, allowing for the crack which has now separated left P^2 and P^3 over 2 mm. beyond their position in life. The wear on P^4 is very similar to that on P^3 , and P_4 must have been, structurally, very like P_3 , except for its surprising antero-posterior shortness, as it was apparently only about 22 mm. long, on each side, which is markedly shorter than either P_2 or P_3 . This is a very unusual character, but the inference is almost inescapable, unless one assumes that the dP_4 s had been retained, but were reduced to short teeth by interproximal wear (Wood, 1938). The total antero-posterior length of P_{2-4} , over all, must have been close to 83 mm.

¹ The principles of occlusion as applied to rhinoceroses have been discussed elsewhere (Wood, 1934).

MEASUREMENTS

The measurements, in millimeters, follow, compared with those of a cast (A.M.N.H. No. 26972) of Borissiak's figured specimen (Borissiak, 1924, Pl. I, fig. 6), No. 1441-3 a-g (Beliajeva, 1928, p. 244) which is similar in stage of wear, and with those of *Trigonias gregoryi*, which is also little worn and of similar size. The general resemblance of the pre-molars of *Cooperia* to those of *Trigonias* has already been emphasized (cf. Fig. 5, A, B and C).

	<i>Cooperia</i> <i>totadentata</i> , type, A.M. No. 20116		<i>Indrico-</i> <i>therium</i> <i>asiaticum</i> Borissiak, cast, A.M. No. 26972	<i>Trigonias</i> <i>gregoryi</i> Wood (1927), type, A.M. No. 13226a	
	Right	Left	Right	Right	Left
I ² A.P.		est. 15.1			
I ² Tr.		est. 18.4			
I ² , circumference at neck		51.0			
I ³ A.P.		14.4			
I ³ Tr.		14.7			
I ³ , circumference at neck		45.0			
I ³ , height of crown		15.4			
C ¹ A.P.	24.5				12.5
C ¹ Tr.	21.2				7.5
C ¹ , circumference at neck	70.0				
C ¹ , height of crown	26.3				7.5
P ¹⁻⁴	108.5	107.0		114.0	115.0
P ²⁻⁴	85.7	81.4	151.9	88.5	88.5
Diastema	29.8	28.0		37.0	37.0
P ¹ A.P.	24.2	24.2		26.0	25.5
P ¹ Tr.	20.5	19.0		23.0	24.0
P ² A.P.	22.9	23.2	40.9	27.5	27.5
P ² Tr.	29.8	30.0	51.0	35.0	35.0
P ³ A.P.	26.3	26.3	50.9	29.0	29.5
P ³ Tr.	38.5	38.4	71.0	45.0	44.5
P ⁴ A.P.	31.0	30.2	57.5	32.0	31.0
P ⁴ Tr.	45.4	45.7	79.1	50.0	50.0
Estimated length nasal incision	101.0				
Probable original depth, dorsum of nasals to Paracone of P ²	195.0				

DISCUSSION

It is obvious from the description and illustrations that the taxonomic and phylogenetic allocation of this form involves difficulty in interpreting its apparently contradictory characters. The broadly diagnostic features are:

1.—The complete placental formula for the upper dentition, as any number of molars other than three is of negligible probability. This set most probably occluded with a complete lower dentition.

2.—A rather stubby, reasonably enlarged but not hypertrophied upper canine, associated with a full set of upper incisors, which are certainly not degenerate, but none of which are demonstrably hypertrophied. This type of front teeth would fit best into any other family of rhinocerotoids than the Rhinocerotidae.

3.— P^2-4 of primitive true rhinoceros pattern, suggesting, especially, *Trigonias* and the baluchitheres, but which may also be compared with other primitive rhinocerotids.

4.—A very primitive P^1 , suggestive of *Ephyrachyus cristalophus*, or of still more primitive perissodactyls.

5.—A snout differing from any other rhinoceros, but with elusive resemblances in various directions.

6.—“Pre-orbital pits,” which are probably, but not demonstrably, artifacts due to crushing.

7.—Premaxillaries apparently somewhat deflected.

The following hypotheses might be offered, to interpret this specimen:

1.—It is an amynodont.

2.—It is a hyracodont.

3.—It is a distinct, coördinate line, deserving familial distinction.

4.—It is a stem rhinocerotoid, in which case it should fit (or be forced) into the Hyrachyidae.

5.—It is a true rhinoceros,

(a) with no close relationship to any other known form.

(b) morphologically ancestral to *Allacerops*.

(c) morphologically ancestral to typical later forms, such as *Trigonias*.

(d) more or less ancestral to the baluchitheres.

Evidences for the amynodont hypothesis are the full set of front teeth (also found elsewhere), the enlarged canine, the curved incisor roots (characteristic of *Amyndodon*, but found wherever the roots are too long for the depth of the premaxillary), the dorsal profile of the nasals (but not their length), and the antorbital hollows (which are certainly largely due to crushing and may be entirely so). Opposed to the amynodont hypothesis are the lack of retraction of the nasals and of any other certain amynodont characters, the lack of any real hypertrophy of the

upper canine and, almost certainly, of the lower canine as well, the lack of any tendency toward reduction of the incisors, the simple crown of I^3 , and almost every character of the premolars, which lack all amynodont features, such as reduction in number and atrophy in size, which are fairly pronounced in even the most primitive species of *Amynodon* (including "*Orthocynodon antiquus*").¹ No known amynodont (including the undescribed Mongolian forms) has four upper premolars. Four deciduous premolars are present in a number of the more primitive forms, and occasionally a battered dP^1 may be found still in place as the permanent premolars erupt. However, it does not function with them, and, in any case, it bears no resemblance to the P^1 of *Cooperia* which is even less worn than the slightly worn P^2 , instead of much more worn as a dP^1 would be. After revising the known amynodonts (ms. essentially complete except on the Mongolian material), I have no hesitation in dismissing the hypothesis that *Cooperia* is an amynodont as of too low an order of probability for further discussion, in spite of its superficial attractions.

Except on a purely verbalistic basis, the hyracodont hypothesis is equally unattractive. No hyracodonts of this size are known, and large ones would be particularly unlikely to occur in Eocene deposits, where known representatives are smallest. The hyracodont canine is never as prominent as this and usually shows more or less reduction. The round, curved root of I^2 would be unlikely to expand into the transversely widened crown of *Hyracodon* or *Ardynia*. The nasals never show this sweep but are characteristically short. The premolars are always of different proportions, being more nearly square rather than rectangular as in *Cooperia* and various true rhinoceroses. Finally, there are no specifically hyracodont features. The one argument for reference to the Hyracodontidae is that it would require least verbal modification of the family definition to include it here, at the cost, however, of a serious actual distortion of the family.

To justify the hypothesis that *Cooperia* belongs to a distinct line co-ordinate with the other families, would require, at the least, both evidence from a more complete specimen and a line of ancestors or descend-

¹ There is evidence in various of Matthew's later writings that, at least at times, he considered the amynodonts as roughly ancestral to the true rhinoceroses. If so, he presumably based this concept either on the restoration of "*Orthocynodon antiquus*" (Scott and Osborn, 1893, Fig. 1) or, possibly, on this restoration in conjunction with the Mongolian specimen described in this paper. Although the inferences made by Scott and Osborn were natural and, perhaps, inevitable in the light of current knowledge (Marsh's skull of *A. advenus* had not yet been prepared) a number were incorrect and the distinctive primitive rhinocerotoid (as opposed to primitive amynodont) characters in their restoration, on which Matthew presumably relied, having been based on misinterpretation, are not actually present in the specimen. In fact, "*O. antiquus*" is specifically inseparable from *A. advenus*. Evidence for this summary statement will be published elsewhere. There is no reason to regard any amynodont as ancestral to any non-amynodont rhinoceros.

ants. Moderately isolated forms near a common stem should not be erected into family rank.

Allocation to the Hyrachyidae has even less in its favor. The front teeth do not exclude it from the group, but the premolars, although showing the V pattern, are advanced over the hyrachyid grade, in fusion of the parastyles, fusion of paracone and metacone into an ectoloph, in the development of the metaconules, as well as in less tangible characters. The curves of the nasals and the depth of the nasal incision are also not hyrachyid, although readily derivable from that condition.

Assignment of *Cooperia* to the true rhinoceroses agrees with the skull and premolar characters. It is apparently, however, more or less in contradiction to the characters of the front teeth, even as recently redefined (Wood, 1927, p. 9). However, the definition of the front teeth of the Rhinocerotidae has been progressively emended, during the present century, to cover *Trigonias*, the baluchitheres and *Allacerops*, so that very little further stretching is required to admit *Cooperia*. It is obvious, except to a creationist, that the progress of discovery is bound to require such emendations. It is entirely possible that the Rhinocerotidae are now becoming an unwieldy group which would benefit by further subdivision, but such subdivision would be premature at the present moment.

The next problem is to evaluate the probability of subhypotheses a, b, c and d (see above). The rather negative subhypothesis (a) that *Cooperia* is a sort of Mahomet's coffin with no close relationship with any known form, will, of course, be sustained only if all attempts to connect it with other forms fail. The hypothesis of ancestry to *Allacerops* has much to commend it at first sight, except the large size of *Cooperia*, especially for its age. The negative evidence consists in an undescribed form in the Shara Murun which seems to meet all the requirements for ancestry to *Allacerops*, and which, in turn, seems structurally derivable from an undescribed form in the Irдин Manha which is fairly different from *Cooperia*. There may have been some relationship between these two forms but hardly a close one.

Ancestry to typical true rhinoceroses such as *Trigonias* is a tempting hypothesis, in view of the long search for such forms and the more or less conflicting and disputed claims of *Prohyracodon*, *Eotrigonias* and *Caenolophus*. P²⁻⁴, if found isolated, would certainly have been considered a new Mongolian species of the genus *Trigonias* (cf. Fig. 5A and B), and far-reaching (and incorrect) conclusions might have been drawn from this erroneous identification. The difficulties with the hypothesis of

ancestry to the true rhinoceroses in general are that the front teeth show no evidence of such relationship, as would be expected in an Upper Eocene form, that the animal seems larger than would be expected and that the snout does not seem to be evolving in the right direction. None of these difficulties, however, exclude descent without any great modification from such a generalized rhinocerotid, which might be ancestral to the rest of the family (except, perhaps, *Allacerops*).

There are a number of resemblances which favor an ancestral relationship to the baluchitheres, without, of course, interfering with the concept of descent from such a stem form as that suggested in the preceding paragraph. The somewhat downwardly-turned anterior tips of the premaxillaries, apparently not caused by crushing, would, if exaggerated, give rise to the most characteristic feature of the baluchithere skull other than its size. The dorsally convex curve of the nasals, if moderately exaggerated, would become that of *Baluchitherium* as restored by Granger and Gregory (1936, Fig. 1). Similar exaggeration would produce the baluchithere type of nasal incision.

The baluchithere enlarged upper incisor can be homologized with I¹ in *Trigonias* with considerable confidence. Thus A.M.N.H. No. 521 (*Subhyracodon trigonodus*, Osborn, 1898, Figs. 25B and 34C), *Epia-ceratherium bolcense* (Dal Piaz, 1930, Pl. XIII, figs. 13-15), an undescribed, loose I¹ in the Bâle collections and other material, apparently show that the original component of I¹ is a sharp conical cusp forming the front end of the typical enlarged incisor. At this stage, it would give the baluchithere condition by further enlargement, without other change. After that, in the typical rhinocerotid course of evolution, an antero-posterior heel forms behind the cusp, as a new structure, after which the root expands under the heel, the heel becomes as high as the original cusp and becomes confluent with it, giving the characteristic rhinocerotid structure. This antero-posterior elongation by adding a heel occurs only in the rhinocerotids, as any enlargement in the hyrachyids or hyracodonts takes the form of a transverse, semi-spatulate blade. Boris-ziak (1924, Pl. I, fig. 8b) shows a curving root for what must be I¹ of *Indricotherium* which would conform roughly to the curving root of I² and to the probable curve of I¹ of *Cooperia*. It seems less difficult, in all, to derive the enlarged, conical baluchithere I¹, without I² or I³, followed by a minute canine, from *Cooperia* than from any more specialized form.

The premolars closely approach the baluchithere pattern, which they would attain with a very slight advance. The baluchitheres are already

so large when they first appear¹ that one would expect that, even as early as the Irдин Manha, an ancestral baluchithere would be at least as large as *Cooperia*. In fact, the criticism might legitimately be made that *Cooperia* is not quite specialized enough to be an Upper Eocene incipient baluchithere, especially with the foregoing description of an Ulan Gochu form which already apparently possessed the majority of the baluchithere diagnostic characters. (The Houldjin appears to be about Middle Oligocene, perhaps about equivalent to the upper portion of the "Oreodon Beds," or possibly a shade later; the Ulan Gochu is Lower Oligocene; and the Shara Murun and Irдин Manha are both Upper Eocene, in a broad sense, the Shara Murun being Upper Uinta to latest Eocene, and the Irдин Manha certainly representing some phase, neither the earliest nor the latest, of the Upper Eocene.) Granger and Gregory (1936) point out that *Allacerops turgaica* could be a structural ancestor of the baluchitheres. They use *Allacerops*, quite justifiably, as the most primitive rhinocerotid of which most of the skeleton is known, but it is obvious that it is not the actual ancestor. At the present moment, the baluchitheres lack an ancestor and *Cooperia* lacks descendants, unless this inferred relationship is correct.

¹ The earliest previously described remains of baluchitheres are from the Houldjin and its equivalent, the Baron Sog, in Mongolia and from the *Indricotherium* Beds of Turkestan which are supposedly of equivalent age. An enormous right radius, A.M.N.H. No. 26026, field No. 772, was collected by Liu Ta Ling, July 8, 1928, in the middle gray layer of the Ulan Gochu Formation at Urtyn Obo. Its length is 1041 mm. which accords with a length of 1200 mm. for the radius of *Baluchitherium grangeri* No. 26166 which belongs to the next to the largest size grade (Granger and Gregory, 1936, p. 38), and 1120 mm. for the field measurement of the radius of A.M.N.H. No. 26386 (the radius was not collected) which belongs to the smallest size grade. Besides the approximate agreement in size, there is rough agreement in general character. All other conceivable interpretations (proboscidian, amynodont, embolother, chalicother) can be eliminated with entire confidence. The field reference to *Embolotherium* breaks down on the lack of titanother characters, to say nothing of a size twice that of Chadron titanother radii. Although this radius (A.M.N.H. No. 26026) is generally rhinocerotid, it shows no special resemblance to any rhinoceros (including such primitive forms as *Hyrachyus*, *Allacerops* and *Trigonas*) except *Baluchitherium*. The general resemblances to *B. grangeri* are obvious from the photographs (Figs. 6-7): it is worth emphasizing the common possession of a much more sharply defined oblique line than in other rhinoceroses (Fig. 6) which presumably marks the upper boundary of the origin of the abductor pollicis longus. There are a number of differences from *Baluchitherium*; the most striking is that the radius, although more than five-sixths as long, is so much slenderer, having a circumference of 301.5 mm. around the middle of the shaft, compared with 500.7 mm. for the corresponding measurement of A.M.N.H. No. 26166. The coronoid process is much more prominent in the earlier form, suggesting somewhat greater flexibility at the elbow. The distal end also shows differences: there is a large well-marked groove presumably for the tendon of the extensor carpi radialis, and a smaller groove medial to it, presumably for the abductor pollicis longus, which, as in rhinoceroses and tapirs, should insert on metacarpal II. These grooves are not defined in *B. grangeri*, not, presumably, because the muscles were smaller, but perhaps because of more limited flexure of the wrist in the bulkier animal, an inference which is partially confirmed by the presence of a well-defined groove for the tendon of the extensor carpi radialis in such more or less primitive and diverse genera as *Hyrachyus*, *Allacerops*, *Trigonas* and *Amyndon*. The carpal articulations also differ: the facettes for the carpals are more sharply distinct and more deeply impressed, not only absolutely, but also relatively, in A.M.N.H. No. 26166 than in 26026, which accords with what must have been a much greater body weight. The total impression from the comparison of these two radii is of an animal which, while well on the road to being a baluchithere, was considerably more primitive, and had a more nearly normal, cursorial habitus, in contrast to the graviportally modified cursorial habitus of *Baluchitherium*. It is a curious fact that in general proportions, although not in size or detailed character, this radius compares best with *Moropus*, which presumably has no other significance than that they belong to perissodactyls with forearms elongated to a similar degree. I abstain, deliberately, from erecting a new name for this radius.

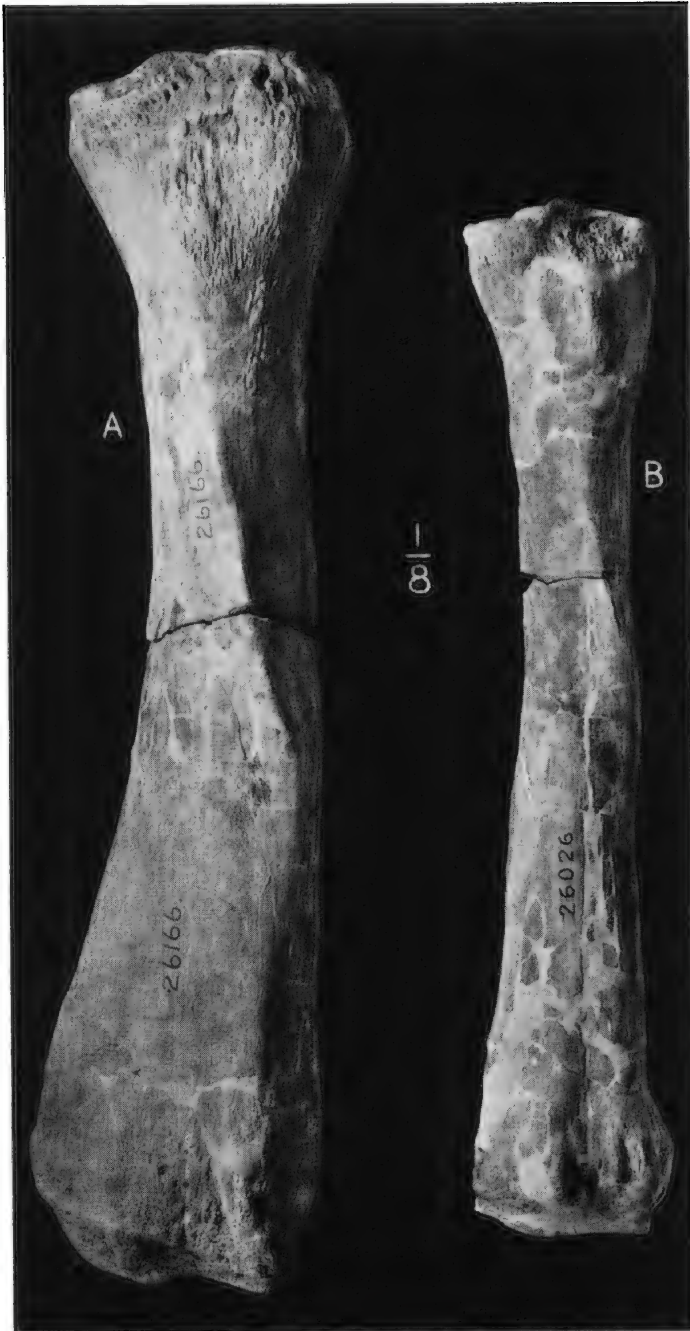


Fig. 6. Right radius, anterior aspect, $\times \frac{1}{8}$. A, *Baluchitherium grangeri*, A.M.N.H. No. 26166. B, *Baluchithere* from Ulan Gochu, A.M.N.H. No. 26026.

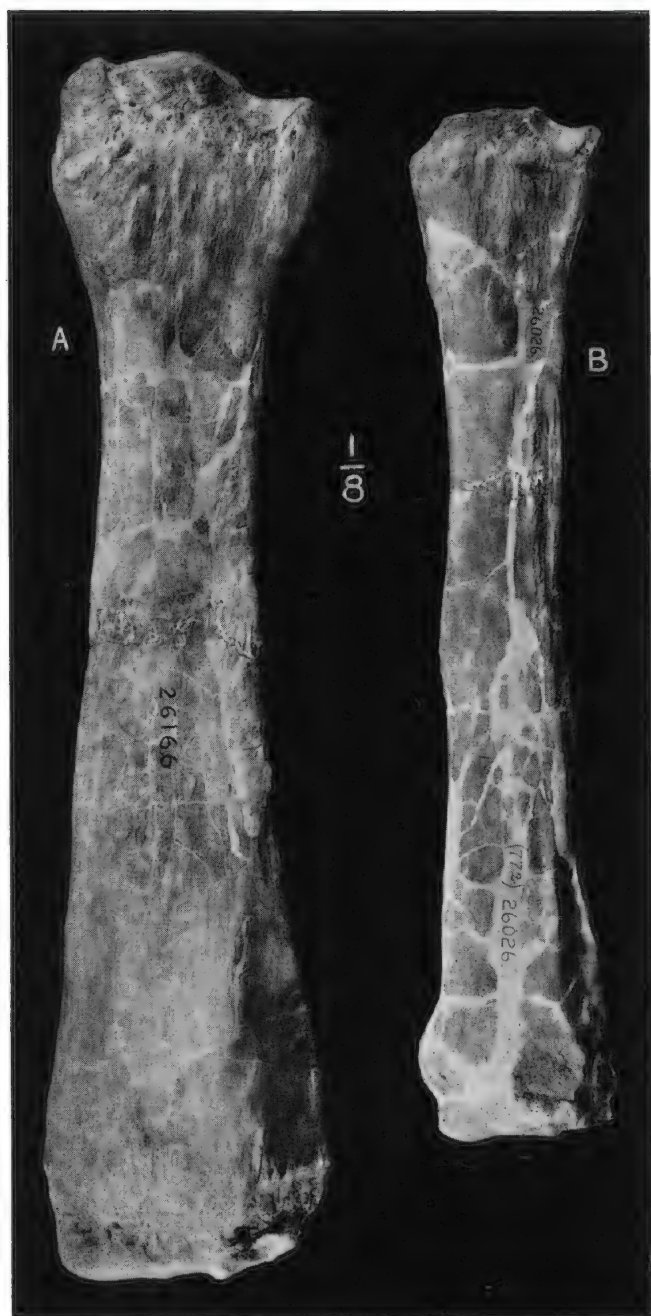


Fig. 7. Right radius, posterior aspect, $\times \frac{1}{8}$. A, *Baluchitherium grangeri*, A.M.N.H. No. 26166. B, *Baluchithere* from Ulan Gochu, A.M.N.H. No. 26026.

For *Cooperia* to become a baluchithere, the following changes would be necessary:

1.—Considerable increase in size. (Changes 1-3, however, would be even more marked in case of derivation from any other conceivable Eocene ancestor.)

2.—Exaggeration of characters of nasals and nasal incision which are already present.

3.—Increased deflection of the tips of the premaxillaries. It is obvious that the deflected baluchithere premaxillaries are associated with the similar deflection of the tip of the mandible and the large lower incisor, presumably I_2 . This deflection of the mandible and I_2 of *Baluchitherium*, as shown by the Mongolian collections, is much less marked in young than in older specimens. It seems possible, then, that this deflection was only partly genetically controlled, but was aggravated, during the adult life of the individual, beyond the condition that would have been genetically established, by some peculiar stress in the feeding habits. This is, of course, entirely hypothetical, but it is certain that one can match just such bone-deformations of the incisive region of the mandible in human "before-and-after" cases apparently attributable to an abnormal degree of continual forward pushing with the tongue. If this interpretation is correct, the premaxillary region of a young baluchithere would be more like *Cooperia* than older individuals which are alone represented in the collections by the famous American Museum skull (A.M.N.H. No. 18650) although indirectly confirmed by complementary lower jaws.

4.—Hypertrophy of I^1 , loss of I^{2-3} , great reduction in size of C^1 to conform to the rudimentary alveolus present in A.M.N.H. No. 18650, the type of *B. grangeri*.

5.—Considerable progress by P^1 .

6.—Inconsiderable progressive advances of P^{2-4} (principally in smoothing the external surfaces of the ectolophs).

7.—Although the lower premolars are short in the baluchitheres, there is no precedent for the extreme shortness of P_4 in comparison with P_2 and P_3 , as inferred for *Cooperia*. This inference, however, is supported by the wear patterns of the ectolophs of P^3 and P^4 on both sides. It might be due to failure to replace the two dP_4 s with their consequent extreme attrition in interproximal wear against the adjoining teeth, but there is no definite evidence for such an interpretation.

The interpretation of ancestral relation to the baluchitheres seems more probable than the only likely alternative which would deny special relationship to any known form. The presence of a baluchithere radius, A.M.N.H. No. 26026, in the Ulan Gochu (Lower Oligocene) helps somewhat to bridge the time gap between *Cooperia* and its supposed descendants.

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ADDENDUM TO AMERICAN MUSEUM *Novitates* No. 1012

Professor T. D. A. Cockerell of the University of Colorado and Paul H. Oehser of the United States National Museum have courteously informed me that *Cooperia* Wood, 1938, Mammalia, is preoccupied by *Cooperia* Ransom, 1907, Nematoda.

Forstercooperia is proposed in its place so that the genotype becomes *Forstercooperia totadentata* (Wood).

Horace Elmer Wood, 2nd.

February 23, 1939

